Lepidoptera from the boreal mixedwood forest in east-central Alberta: comparison of assemblages from a mature stand and an old stand

G.R. Pohl, D.W. Langor,
J.-F. Landry, and J.R. Spence

INFORMATION REPORT NOR-X-396
Northern Forestry Centre

Natural Resources Canada
Canadian Forest Service

Ressources naturelles Canada
Service canadien des forêts

Canada

The Canadian Forest Service's Northern Forestry Centre is responsible for fulfilling the federal role in forestry research and technology transfer in Alberta, Saskatchewan, Manitoba, Nunavut, and the Northwest Territories. The main objective is research in support of improved forest management for the economic, social, and environmental benefit of all Canadians.

The Northern Forestry Centre is one of five centers of the Canadian Forest Service, which has its headquarters in Ottawa, Ontario.

Le Service canadien des forêts, Centre de foresterie du Nord, représente le gouvernement fédéral en Alberta, en Saskatchewan, au Manitoba, au Nunavut et dans les Territoires du Nord-Ouest en ce qui a trait aux recherches forestières et au transfert de technologie. Cet organisme s'intéresse surtout à la recherche en vue d'améliorer l'aménagement forestier afin que tous les Canadiens puissent en profiter aux points de vue économique, social et environnemental.

Le Centre de foresterie du Nord constitue l'un des cinq établissements du Service canadien des forêts, dont l'administration centrale est à Ottawa (Ontario).

Cover shows various Lepidoptera found in the east-central Alberta boreal mixedwood forest.

105-00803/

LEPIDOPTERA FROM THE BOREAL MIXEDWOOD FOREST IN EAST-CENTRAL ALBERTA: COMPARISON OF ASSEMBLAGES FROM A MATURE STAND AND AN OLD STAND

G.R. Pohl, D.W. Langor, J.-F. Landry,[1] and J.R. Spence[2]

INFORMATION REPORT NOR-X-396

Canadian Forest Service
Northern Forestry Centre
2004

[1] Agriculture and Agri-Food Canada, Eastern Cereal and Oilseed Research Centre, Ottawa, Ontario K1A 0C6.
[2] Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2E9.

© Her Majesty the Queen in Right of Canada, 2004
Catalogue No. Fo46-12/396E
ISBN 0-662-38075-4
ISSN 0831-8247

This publication is available at no charge from:
Natural Resources Canada
Canadian Forest Service
Northern Forestry Centre
5320-122 Street
Edmonton, Alberta T6H 3S5

A microfiche edition of this publication may be purchased from:
Micromedia Proquest
20 Victoria Street
Toronto, Ontario M5C 2N8

TTY: 613-996-4397 (Teletype for the hearing-impaired)
ATS: 613-996-4397 (appareil de télécommunication pour sourds)

Library and Archives Canada Cataloguing in Publication

Main entry under title :

Lepidoptera from the boreal mixedwood forest in east-central Alberta: comparison of assemblages from a mature stand and an old stand

(Information report ; NOR-X-396)
Includes bibliographical refrences.
Includes an abstract in French.
ISBN 0-662-38075-4
Cat. no. Fo46-12/396E

1. Lepidoptera – Ecology – Alberta.
2. Forest insects – Ecology – Alberta.
3. Forest ecology – Alberta.
4. Environmental indicators – Alberta.
I. Pohl, Gregory Ray, 1965- .
II. Northern Forestry Centre (Canada)
III. Series: Information report (Northern Forestry Centre (Canada)); NOR-X-396.

QL552.L44 2004 595.78 C2004-980279-8

This report has been printed on Canadian recycled paper.

Pohl, G.R.; Langor, D.W.; Landry, J.-F.; Spence, J.R. 2004. *Lepidoptera from the boreal mixedwood forest in east-central Alberta: comparison of assemblages from a mature stand and an old stand.* Nat. Resour. Can., Can. For. Serv., North. For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-396.

ABSTRACT

The Lepidoptera specimens collected in light traps in two *Populus*-dominated stands in central Alberta, one mature (52 years old) and the other old (>120 years old), were compared. This represents the first detailed examination of these communities, and thus it adds considerable new information on the distribution of arthropods in the boreal forest. In total, 393 species were collected, from an overall regional forest assemblage estimated to contain 481 species. Comparisons of abundance, richness, and diversity were complicated by large year-to-year differences. The indicator value of each common species was assessed; 19 species were deemed to be mature-stand associates and 28 species were deemed to be old-stand associates. More of the old-stand associates were monophagous than was the case for the mature-stand associates. More species unique to a stand were captured in the old stand than in the mature stand. The more specialized community in the old stand is thought to reflect the higher structural complexity of that stand. Many mature-stand and old-stand associates fed on plants that were abundant in both stands, which suggests that they were not limited by host-plant availability. Common species were tested for evenness of distribution across sites, according to a formula developed and presented here; by this measure, 38 species were deemed to be stand generalists. The stand generalists included a greater proportion of polyphagous species than the mature-stand and old-stand specialists. On the basis of the evidence presented here, the macrolepidoptera show promise for use as biodiversity indicators. The Geometroidea and Drepanoidea in particular include many species with strong indicator value for old-growth specialization.

RÉSUMÉ

Cette étude a comparé les spécimens de lépidoptères capturés dans des pièges lumineux dans deux peuplements dominés par des peupliers (*Populus*) du centre de l'Alberta, à savoir dans un peuplement mûr (de 52 ans) et dans un vieux peuplement (de plus de 120 ans). Elle constitue le premier examen détaillé de ces communautés et, par conséquent, enrichit considérablement les données sur la répartition des arthropodes en forêt boréale. Elle a permis de récolter un total de 393 espèces dans un assemblage forestier régional général estimé à 481 espèces. Les différences considérables relevées d'une année à l'autre ont compliqué les comparaisons de l'abondance, de la richesse spécifique et de la diversité. On a évalué la valeur indicatrice de chaque espèce commune; 19 d'entre elles ont été jugées comme des espèces associées au peuplement mûr et 28 autres, comme des espèces de vieux peuplement. Ce dernier abritait un plus grand nombre d'espèces associées monophages que le peuplement mûr. Le nombre d'espèces capturées exclusivement dans un peuplement était plus élevé dans le vieux peuplement que dans le peuplement mûr. La communauté plus spécialisée du vieux peuplement refléterait la plus grande complexité de la structure de ce peuplement. Nombre d'espèces associées à l'un et l'autre des peuplements s'alimentaient sur des espèces végétales qui étaient abondantes dans les deux peuplements, ce qui laisse supposer que la disponibilité des plantes hôtes n'est

pas un facteur limitant. Une formule qui est explicitée et présentée dans ce rapport a permis de vérifier l'uniformité de répartition des espèces communes d'une station à l'autre et de déterminer que 38 espèces étaient des généralistes. Ces dernières regroupaient une plus grande proportion d'espèces polyphages que les espèces spécialistes du peuplement mûr et du vieux peuplement. D'après les données qui sont ici présentées, il semblerait que les macrolépidoptères soient prometteurs comme indicateurs de la biodiversité. Les Geometroidea et les Drepanoidea regroupent notamment de nombreuses espèces pouvant servir de très bon indicateur de la spécialisation à l'égard des vieux peuplements.

CONTENTS

INTRODUCTION 1

MATERIALS AND METHODS 1
- Study Area 1
- Collection, Curation, and Identification of Lepidoptera 2
- Statistical Analyses 2
- Habitat Association Criteria 3

RESULTS 3
- Temporal Variability 4
- Within-Stand Variability 5
- Variability Associated with Stand Age 5
- Mature-Stand and Old-Stand Associates 10

DISCUSSION 15
- Comparison of Mature and Old Stands 15
- Utility of Lepidoptera as an Indicator Group 15
- Implications for Forest Harvesting 18

ACKNOWLEDGMENTS 18

LITERATURE CITED 18

FIGURES

1. Total species counts and number of shared and unique Lepidoptera species collected in individual traps within stands in 1994 5
2. Rarefaction estimates of species richness in subsamples of 650 individuals and Chao-1 estimates of species richness of Lepidoptera at two mature sites and two old sites in 1994 6
3. Rarefaction estimates of Lepidoptera species richness based on individual trap catches in 1994 7
4. A) Standardized abundance B) Chao-1 estimated species richness of Lepidoptera in mature and old stands in 1993, 1994, and 1995 8
5. Rarefaction estimates of Lepidoptera species richness in mature and old aspen stands in 1993, 1994, and 1995 9
6. Rarefaction estimates of Lepidoptera species richness in subsamples of 250 specimens from mature and old aspen stands in 1993, 1994, and 1995 9
7. Number of shared and unique species collected in mature and old stands in 1993, 1994, and 1995 11
8. Cluster analysis of Bray–Curtis pair-wise percent similarities for Lepidoptera collected in 1993, 1994, and 1995 11

TABLES

1. Number of species and individuals of Lepidoptera identified from ultraviolet light trap catches, arranged by superfamily 4
2. Annual summary of Lepidoptera abundance and species richness, 1993 to 1995 4
3. Abundance and indices of diversity for Lepidoptera collected in two mature sites and two old sites in 1994 6
4. Indices of diversity for Lepidoptera collected in mature and old stands in 1993, 1994, and 1995 6
5. Common species of Lepidoptera associated with aspen-dominated stands near Lac La Biche, Alberta 12
6. Numbers and percent of mature-stand and old-stand associates and of generalists, categorized by degree of host-plant specialization 14
7. Numbers and percent of mature-stand and old-stand associates and of generalists, categorized by host-plant guild 14
8. Average indicator value[1] and generalist value, and number and percent of species designated as mature-stand and old-stand associates and as generalists, for taxonomic subgroups of Lepidoptera 17

INTRODUCTION

The biota of the boreal mixedwood forest is dominated by a diverse but relatively poorly studied arthropod fauna. There are an estimated 22 000 species of insects in Canada's boreal forest (Danks and Foottit 1989). For described species that are not significant pests little is known other than the name, and an estimated 45% of insect species inhabiting the boreal region have not yet been described (Danks 1979; Danks and Foottit 1989). Many of these species are known to have affinities for particular microhabitats within the forest, particularly for structurally complex old stands (Niemelä et al. 1993a, 1993b; Spence et al. 1996; Beaudry et al. 1997).

Succession and stand development in these forests have historically been driven by natural fire events (Bonan and Shugart 1989), which has resulted in a mosaic of stands of various ages across the landscape (Peterson and Peterson 1992). However, in the past two decades, industrial logging has emerged as a primary disturbance and stand initiator (Pratt and Urquhart 1994). There is concern that the relatively short (60–70 years) and homogeneous rotations currently envisioned by the forest industry will reduce the frequency of older seral stages (Maser 1994) and thus adversely affect their constituent species. These projections have in turn given rise to concerns about the sustainability of intensifying these practices, especially with regard to biodiversity.

Unfortunately, there is little baseline information available to describe the impacts of current mixedwood management practices on either the diverse biota of these forests or the integrity of the forest ecosystem. Thus, a collaborative study was carried out from 1991 to 1995 to examine the structure, composition, and biodiversity of aspen-dominated mixedwood stands of different ages in Alberta. A major objective of this work was to inventory biota associated with specific forest successional stages and, in particular, to identify taxa that might be strongly linked to old stands. The taxa sampled included plants and vertebrates (Stelfox 1995 and papers therein), epigeic beetles and spiders (Spence et al. 1996, 1997), saproxylic insects (Hammond 1997; Spence et al. 1997; Hammond et al. 2002), and Lepidoptera. The latter were chosen for the study reported here because they serve important roles as herbivores, pollinators, and food for other organisms (Scoble 1992); are easily collected (Young 1997); and are sensitive to forest disturbances (Magurran 1985; Lawton et al. 1998; Morneau 2002). Despite being fairly mobile as adults and prone to population fluctuations (Young 1997), they are arguably the only defoliator group that is well enough known taxonomically for their diversity to be assessed. In the current study, a baseline examination of this assemblage was conducted in a mature stand and an old stand, and attempts were made to identify species that might be unique to old stands and useful as indicators for conservation purposes. As well, the potential for Lepidoptera and its taxonomic subgroups to serve as biodiversity indicators in the boreal forest was examined. This is only the second study of Lepidoptera diversity in the boreal forest of western Canada (see Morneau 2002) and the only one comparing mature and old forest stands.

MATERIALS AND METHODS

Study Area

The two study stands were located near Touchwood Lake, east of Lac La Biche, Alberta (54°51'N, 111°27'W), in the Central Mixedwood subregion of the Boreal Forest Natural Region (Beckingham and Archibald 1996). They represent a subsample of those selected by Stelfox (1995; stands designated therein as Mature 2 and Old 4) for broader study. Both stands were of fire origin, and they were within 5 km of each other. Stand descriptions were derived from a random sample of 30 trees in each stand; ages are based on examination of tree cores.

The 52-year-old mature stand (M2) was growing on a mesic site, was 269 ha in area, and had 2098 ± 279 stems/ha; the closed canopy was 19.8 ± 0.3 m in height, and the mean diameter at breast height was 16.1 ± 0.6 cm. The stand consisted of approximately 95% *Populus* spp. and had a low shrub layer consisting primarily of prickly rose

(*Rosa acicularis* Lindl. [Rosaceae]) and raspberry (*Rubus idaeus* L. [Rosaceae]). The >122-year-old old stand (O4) was growing on a mesic site, was 187 ha in area, and had 635 ± 65 stems/ha; the canopy was 26.7 ± 0.6 m in height, with many gaps due to tree fall, and the mean diameter at breast height was 37.9 ± 1.2 cm. The stand consisted of approximately 70% *Populus* spp. and 30% white birch (*Betula papyrifera* Marsh. [Betulaceae]) and had a high shrub layer consisting primarily of red-osier dogwood (*Cornus stolonifera* Michx. [Cornaceae]), beaked hazelnut (*Corylus cornuta* Marsh [Betulaceae]), and green alder (*Alnus viridis crispa* (Ait.) [Betulaceae]). The structure and understory vegetation of these stands has been described in detail (Stelfox 1995). Two sampling sites were selected at random in each stand, with the restriction that they be at least 200 m from the stand edge and from one another. They are designated as M2-2 and M2-3 (sites in the mature stand) and O4-5 and O4-6 (sites in the old stand), to conform with the studies detailed in Stelfox (1995).

Collection, Curation, and Identification of Lepidoptera

At each of the four sites, Lepidoptera were collected with the aid of a battery-powered 30-W ultraviolet (UV) light trap. In 1993, bottles containing ethyl acetate were placed in the traps to kill the moths, but in 1994 and 1995, solid dichlorvos was used. Traps were set up from dusk to dawn for one night approximately every 2 weeks, from 16 June to 16 September in 1993, from 3 May to 5 October in 1994, and from 28 May to 28 August in 1995.

Moths were removed from the traps, placed in glassine envelopes, and stored at −20°C within 2 days of collection. They were identified to species level by the senior author, with confirmation of problematic species by J.-F. Landry and other taxonomic specialists at the Canadian National Collection (CNC) in Ottawa, Ontario. Higher-level taxonomy follows Kristensen (1999). In cases where the taxonomic knowledge of a group is incomplete, specimens were identified to morphospecies, pending description of new species and revision of the groups in question. Pinned voucher specimens have been deposited at the Northern Forestry Research Collection at the Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, and at the CNC.

Statistical Analyses

Because of large differences in species abundance and composition among years, the 3 years of collection data are treated independently, except for the indicator value and evenness index calculations, for which the 3 years of data were combined. On four occasions, traps failed to operate: 1 July 1993 (sites M2-2 and O4-5), 28 June 1995 (site O4-5), and 27 July 1995 (site O4-5). The 1994 data were used to examine within-stand differences, because they were based on the longest and most complete trapping season. For these comparisons, raw abundances can be compared directly because there were no losses due to trap failures that year. For stand-level information involving other years, abundances were standardized to correct for traps that failed, by dividing catch per stand by the number of operational traps per stand, for each night's trapping.

Species richness was compared by means of rarefaction, a statistical method for estimating the number of species present in random subsamples of different size drawn from a larger sample. The resulting values allow comparison of species richness among samples of different size (Sanders 1968; Hurlbert 1971) and can be interpreted as diversity measures because the method takes into account the number of species as well as their relative abundance. These estimates cannot be extrapolated beyond the sample size to obtain a total richness estimate without assuming a statistical distribution of species abundances (Krebs 1989, page 335). To obtain such an estimate, Chao-1 estimates of diversity (Chao and Lee 1992) were calculated as described by Colwell and Coddington (1994). The rarefaction and Chao-1 estimates were calculated from raw data, using programs published by Brzustowski (1999). To allow comparison of diversity with that reported in other studies, the widely used Shannon–Wiener index of diversity (Pielou 1977) and Simpson's index of diversity as modified by Pielou (1969) were calculated as well.

Beta diversity was calculated by means of Wilson and Shmida's (1984) beta diversity and beta turnover calculations. The former value expresses the average proportion of species, and the latter the average number of species, lost or gained between successive samples. This calculation was deemed by Wilson and Shmida (1984) the most

appropriate of six measures that they compared. The calculation produces a dimensionless number indicating the relative degree of species turnover between sites or along a gradient. It was used here to measure relative species turnover along a temporal gradient.

Sites were compared with pair-wise Bray–Curtis percent similarities (Bray and Curtis 1957; Wolda 1981) calculated from standardized data, in a clustering procedure employing unweighted arithmetic means. These calculations were done with a program published by Brzustowski (1999).

Habitat Association Criteria

To examine individual species for degree of stand type association, data for all 3 years were pooled, with entire dates deleted when one or more traps failed on that day. From these data, indicator values were calculated following the procedure of Dufrêne and Legendre (1997) for all species with an overall abundance of at least 10 specimens. A species was deemed to be associated with a particular stand type if its indicator value was at least 0.75.

To calculate the degree of generalization of individual species, an evenness index was calculated, according to the following formula:

$$E = 1 - (\sum | x_i - \bar{x} | \ / \ 2 (T - T/N))$$

where E = evenness measure for the species in question

x_i = abundance of species at site i

$\bar{x}$ = average abundance of the species across all sites

T = total number of individuals across all sites

N = number of sites

This calculation yields a value between 0 and 1, where 0 represents a situation in which all specimens are clustered at one site, and 1 represents an exactly even distribution of specimens across all sites. This value was calculated for all species with an overall abundance of at least 10 specimens, using the 3 years of pooled data. As in the indicator value calculations, entire dates were deleted when one or more traps failed on that day. Species were deemed to be generalists if their evenness values were at least 0.75.

Host-plant information was gathered for species designated as stand associates and as generalists, primarily from Handfield (1999), Prentice (1962, 1963, 1965), and McGuffin (1967, 1972, 1977, 1981, 1987, 1988), as well as from other sources (Forbes 1923, 1948; McDunnough 1946; Jones 1951; Freeman 1958; Razowski 1966; Munroe 1976; Rockburne and Lafontaine 1976; Sargent 1976; Brown 1980; Morris 1980; Adamski and Peters 1986; Miller 1987; Rings et al. 1992; Lafontaine and Wood 1997; Lafontaine 1998; Hodges 1999). From this information, Lepidoptera species were categorized as monophagous (restricted to a single plant genus), oligophagous (restricted to a single plant family), or polyphagous (known to feed regularly on more than one plant family), similar to Morneau (2002). Species were also categorized into 10 feeding guilds similar to Morneau (2002): grass feeders, woody plant feeders, low and nonwoody plant feeders, fungus and dead leaf feeders, Salicaceae feeders, general deciduous tree feeders, conifer feeders, lichen and moss feeders, root feeders, and generalists.

RESULTS

A total of 9731 specimens were collected, and 393 species belonging to 33 families were identified (Table 1; see Pohl et al. [n.d.] for a complete list). Specimens too damaged to be identified accounted for 3.9% of the catch (382 specimens). The most abundant families were Noctuidae with 3161 specimens (32.5% of the catch) and 102 species and Geometridae with 2164 specimens (22.2% of the catch) and 72 species. The most common species was *Scoparia biplagialis* Walker (Crambidae), with 972 specimens, followed by *Enargia decolor* (Walker) (Noctuidae), with 684 specimens. The numbers of these species varied greatly from year to year; on the basis of the raw data, 86.4% of the former were collected in 1994, and 86.8% of the latter were collected in 1995. Many species were rare: 90 (22.9% of species) were represented by only a single specimen, and 46 (11.7% of species) were represented by just two specimens. The Chao-1 estimate of total species richness was 481 ± 19.8, which suggests that this study revealed about 80% of the entire night-flying lepidopteran assemblage.

Table 1. Number of species and individuals of Lepidoptera identified from ultraviolet light trap catches, arranged by superfamily

Superfamily	No. (and percent)			
	Species		Individuals	
Microlepidoptera				
Eriocranoidea	1	(0.3)	1	(<0.1)
Nepticuloidea	1	(0.3)	1	(<0.1)
Incurvarioidea	1	(0.3)	1	(<0.1)
Tineoidea	6	(1.5)	28	(0.3)
Gracillarioidea	15	(3.8)	170	(1.8)
Gelechioidea	57	(14.5)	469	(5.0)
Yponomeutoidea	13	(3.3)	55	(0.6)
Cossoidea	3	(0.8)	12	(0.1)
Choreutoidea	2	(0.5)	2	(<0.1)
Tortricoidea	63	(16.0)	1152	(12.3)
Urodoidea	1	(0.3)	2	(<0.1)
Pterophoroidea	2	(0.5)	7	(0.1)
Pyraloidea	22	(5.6)	1355	(14.5)
Subtotal	187	(47.6)	3255	(34.8)
Macrolepidoptera				
Lasiocampoidea	2	(0.5)	35	(0.4)
Bombycoidea	2	(0.5)	135	(1.4)
Drepanoidea	6	(1.5)	98	(1.0)
Geometroidea	73	(18.6)	2292	(24.5)
Noctuoidea	123	(31.3)	3534	(37.8)
Subtotal	206	(52.4)	6094	(65.2)
Overall total[a]	393	(100.0)	9349	(100.0)

[a]Does not include 382 individuals that were too damaged to be identified.

Temporal Variability

Species composition changed markedly over the course of a single season. In 1994, the average proportion of species shared between consecutive trap samples was 0.18 in the mature stand and 0.24 in the old stand. Wilson and Shmida's (1984) average beta diversity measure between successive samples was 0.706 for the mature stand, and 0.646 for the old stand. Expressed in terms of species turnover (the number of species lost or gained between successive samples), this results in an average of 6.87 among mature stand catches and 6.32 among old stand catches in 1994.

There was also considerable year-to-year variation. Far fewer specimens and species were collected in 1993 than in 1994 or 1995 (Table 2). This was not merely an artifact of the variable sampling period: when only the trapping period from the middle of June to the end of August was compared, and the values were standardized to the number of operational traps, the abundance (number of individuals) per trap was 41.0, 186.1, and 166.0 in 1993, 1994, and 1995, respectively. The low catch in 1993 was probably due in part to inclement weather encountered during the last two trapping nights that year. However, these data also illustrate the variable nature of the Lepidoptera community from year to year, as seen in the population cycles of individual species such as *S. biplagialis* and *E. decolor*.

Table 2. Annual summary of Lepidoptera abundance and species richness, 1993 to 1995

Year	No. of individuals	No. of species	No. of unique species[a]
1993	759	124	6
1994	4880	305	79
1995	4092	289	75

[a]Species collected only in that particular year.

Only 92 species were common to all 3 years. Average Bray–Curtis percent similarities indicate that there was considerably less similarity between years at the same site (13.1–30.6%) than between sites within a stand in the same year (40.6–66.1%). This year-to-year variation in species composition was probably due to the variable sampling period and the lengthy trapping interval, as well as to the large differences in standardized abundance across years. For these reasons, year-to-year comparisons were not explored further.

Within-Stand Variability

Of the 305 species collected in 1994, only 79 were common to all four sampling locations. Except for *Macaria loricaria* (Evers.) (Geometridae; 66 individuals), which was not collected at site M2-3, all of the most abundant species (38 species, each with at least 30 individuals) were collected at all four sites. In the mature stand and the old stand, 51.9% and 47.0%, respectively, of species were shared between sites within the stand (Fig. 1). Sites M2-2 and O4-6 harbored more species unique to a site than did the M2-3 and O4-5 sites. Most of the species unique to one site in a stand were singletons or doubletons, and none was represented by more than four individuals. Sites M2-2 and O4-6 also had the highest abundance (Table 3) and Chao-1 estimates of species richness (Fig. 2) in their respective stands. Overall, these sites harbored a larger, more diverse fauna than sites M2-3 and O4-5.

The percent similarity among individual site catches within stands was relatively low, at 54.5% and 58.0% for mature and old stands, respectively.

Variability Associated with Stand Age

Lepidoptera abundance in 1994 was highly variable (Table 3), with no clear stand-level trend. These abundances were not dramatically affected by catches of *Scoparia biplagialis*, although this species made up a greater proportion of the catch in the old stands (21.3% in O4-5 and 22.4% in O4-6 versus 12.8% in M2-2 and 9.2% in M2-3). Rarefaction estimates of diversity (Figs. 2 and 3) suggested a slightly richer fauna in the mature stands, although this trend was not always significant. Chao-1 estimates of total species richness (Fig. 2) did not follow this trend; however, the overall Chao-1 richness pattern was similar to that for abundance, which indicates a correlation between these two parameters. Both the Simpson's index and the Shannon–Wiener index (Table 3) indicated that the mature sites had greater heterogeneity.

In all 3 years, standardized abundance (Fig. 4A) appeared to be higher in old stands than in mature stands, but these differences were not significant (*t*-test probabilities were 0.33, 0.83, and 0.22 for 1993, 1994, and 1995 respectively). Rarefaction estimates of species richness (Figs. 5 and 6) and values for Simpson's index and Shannon–Wiener index (Table 4) were higher for old stands than for mature stands in 1993 and 1995, but not in 1994. Chao-1 estimates of species richness were higher for old stands in 1994 and 1995 but higher for mature stands in 1993 (Fig. 4B).

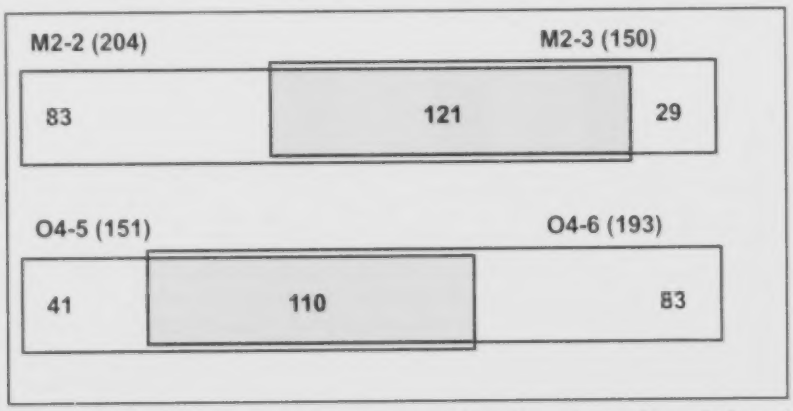

Figure 1. Total species counts (in parentheses) and number of shared (gray portion of bars) and unique (white portions) Lepidoptera species collected in individual traps within stands in 1994 (bar lengths are proportional to the number of species). M2-2 and M2-3 designate sites in the mature stand; O4-5 and O4-6 designate sites in the old stand.

Table 3. **Abundance and indices of diversity for Lepidoptera collected in two mature sites (M2-2, M2-3) and two old sites (O4-5, O4-6) in 1994**

Site	No. of individuals	Index of diversity: Simpson's	Index of diversity: Shannon–Wiener
M2-2	1525	0.970	6.24
M2-3	717	0.977	6.29
O4-5	987	0.943	5.81
O4-6	1651	0.937	5.82

Note: Simpson's ranges from 0 to almost 1 and Shannon–Wiener theoretically ranges from 0 to infinity.

Table 4. **Indices of diversity for Lepidoptera collected in mature and old stands in 1993, 1994, and 1995**

Year and stand type	Index of diversity: Simpson's	Index of diversity: Shannon–Wiener
1993		
Mature	0.939	4.85
Old	0.951	5.45
1994		
Mature	0.973	6.41
Old	0.940	5.98
1995		
Mature	0.930	5.39
Old	0.958	6.01

Note: Simpson's ranges from 0 to almost 1 and Shannon–Wiener theoretically ranges from 0 to infinity.

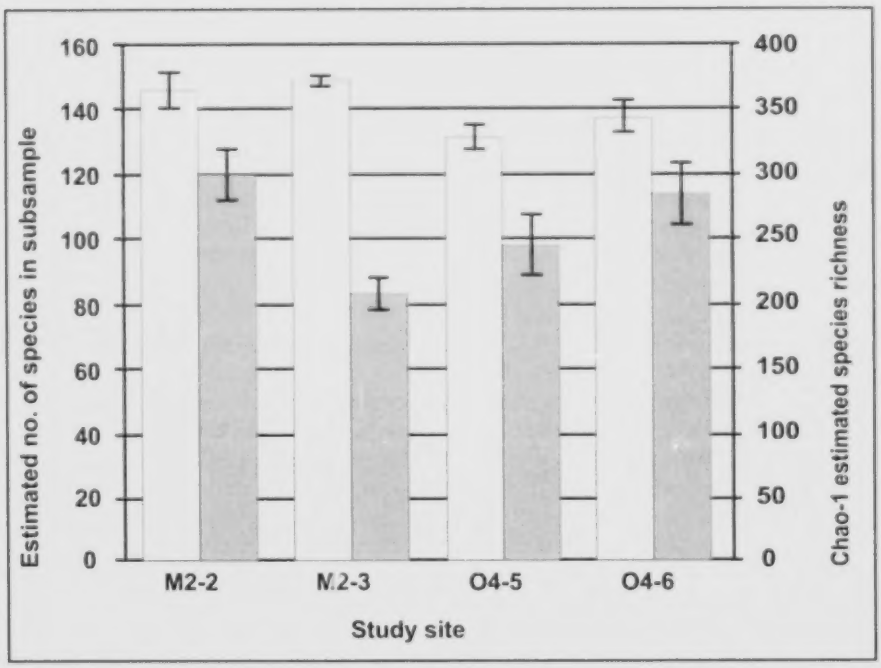

Figure 2. Rarefaction estimates of species richness in subsamples of 650 individuals (white bars, left scale) and Chao-1 estimates of species richness (gray bars, right scale) of Lepidoptera at two mature sites (M2-2, M2-3) and two old sites (O4-5, O4-6) in 1994 (error bars = standard deviations).

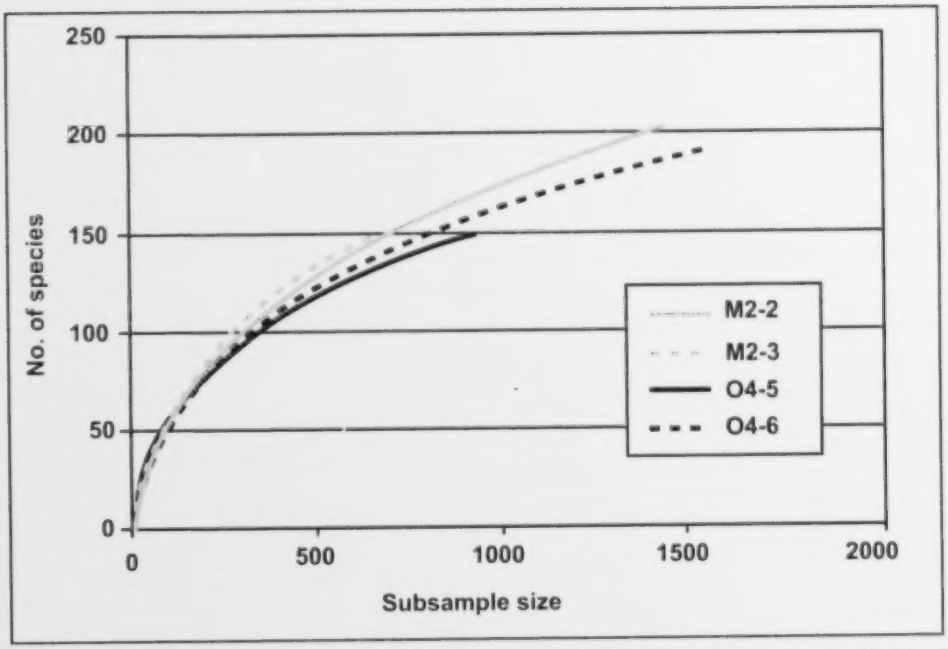

Figure 3. Rarefaction estimates of Lepidoptera species richness based on individual trap catches in 1994. M2-2 and M2-3 designate sites in the mature stand; O4-5 and O4-6 designate sites in the old stand.

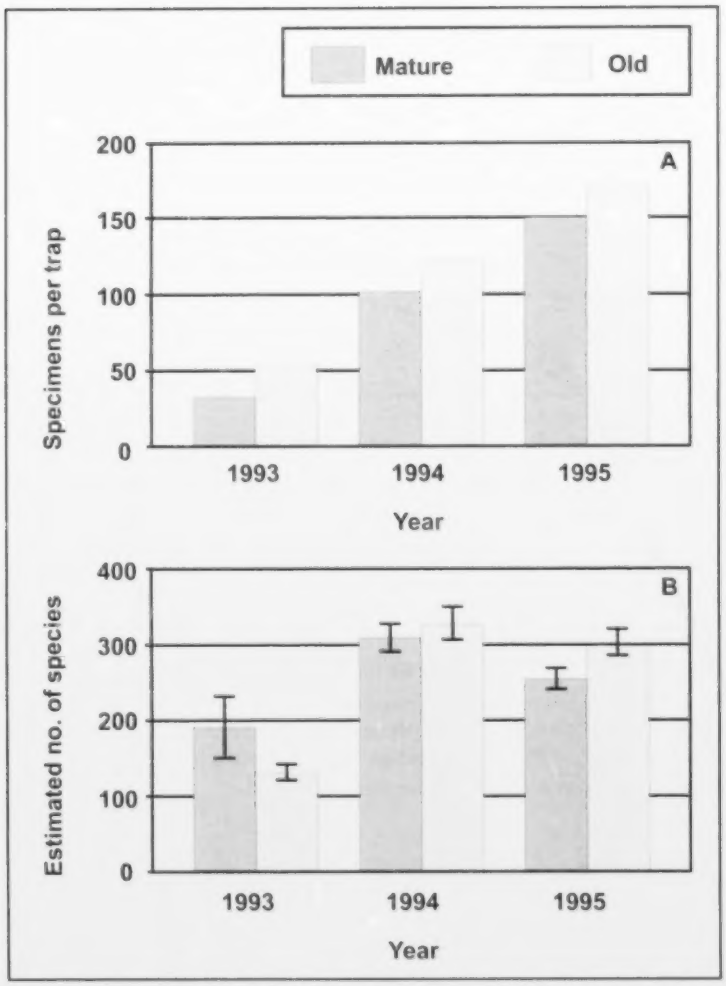

Figure 4. A) Standardized abundance and B) Chao-1 estimated species richness of Lepidoptera in mature and old stands in 1993, 1994, and 1995 (error bars = standard deviations).

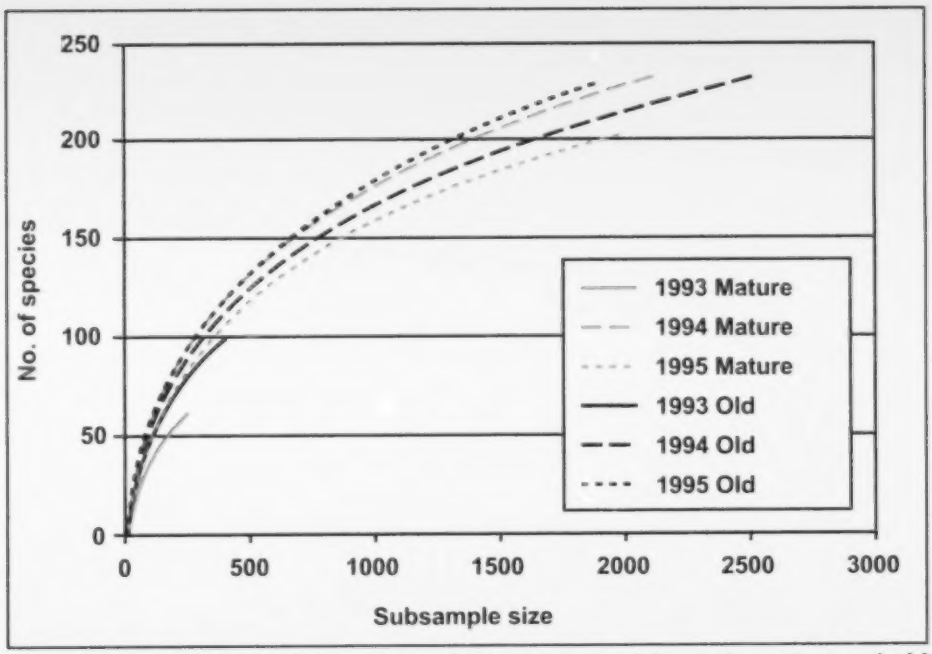

Figure 5. Rarefaction estimates of Lepidoptera species richness in mature and old aspen stands in 1993, 1994, and 1995.

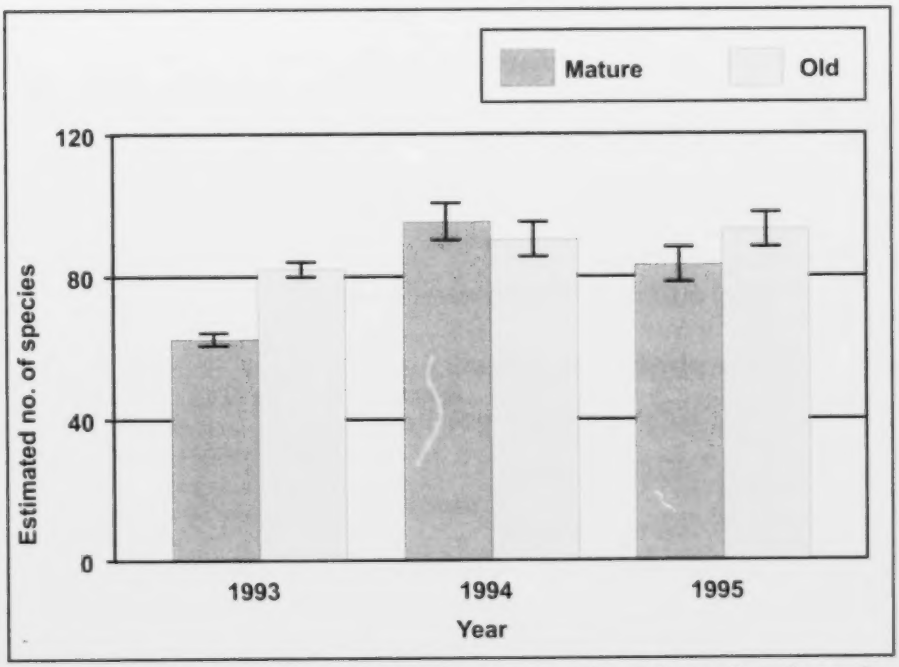

Figure 6. Rarefaction estimates of Lepidoptera species richness in subsamples of 250 specimens from mature and old aspen stands in 1993, 1994, and 1995.

The proportion of species shared between stands was 34.7%, 53.1%, and 50.2% in 1993, 1994, and 1995, respectively (Fig. 7). Thus, species turnover among stands was highest in 1993, resulting in higher β-diversity estimates for that year, undoubtedly because of the low catches in that year (Fig. 7). Bray–Curtis percent similarities between the mature stand and the old stand were 49.4%, 62.7%, and 53.7% for 1993, 1994, and 1995, respectively. Cluster dendrograms (Fig. 8) grouped sites on the basis of stand age only in 1995. The cluster analysis was also done with all uncommon species (less than 10 individuals collected at all four sites) deleted from the matrix. The resulting clustering patterns (not shown) were the same, but there was a shift to higher similarities at the branch points. The clustering algorithm was also done with the most common species in each year deleted from that year's data (*Aplectoides condita* (Guenée) in 1993, *S. biplagialis* in 1994, *E. decolor* in 1995). The result was similar branching patterns for 1994 and 1995, but a switch in the position of M2-3 and O4-6 in 1993. Neither the uncommon species nor a single dominant species appeared to unduly influence the clustering results.

Mature-Stand and Old-Stand Associates

Although 58 species were collected exclusively in the mature stand and 91 were collected exclusively in the old stand over the 3 years of sampling, most of these species were relatively rare (34 singletons and 14 doubletons in the mature stand, 56 singletons and 12 doubletons in the old stand). Many of these may have an affinity for a particular forest type, but a larger sampling effort is needed before that can be asserted with confidence.

Considering only the 130 most abundant species (at least 10 specimens collected), 19 were deemed to be mature-stand associates, 28 were deemed old-stand associates, and 38 were deemed stand generalists (Table 5). Many of the old-stand and mature-stand associates may truly be specialists in a particular stand type; however, their habitat affinities have not been proven, so the term "specialist" has not been used to describe them. The stand generalists made up 26.7% of the total catch in the mature stand and 23.3% in the old stand. The old-stand associates contained the highest number (11) and proportion (39.3%) of monophagous species (Table 6). The stand generalists contained the greatest number (11) and proportion (28.9%) of polyphagous species and the lowest proportion (15.8%) of monophagous species (Table 6).

There were few trends among the mature-stand and old-stand associates and the stand generalists with respect to feeding guilds (Table 7). Grass feeders are clearly not a well-developed group in the boreal forest, although the lone member here (*Lithacodia albidula* (Guenée)) is a common inhabitant of parkland and boreal forest habitats. The fungus and dead leaf feeders are a specialized group exhibiting considerable evolutionary adaptation. This feeding mode has not arisen often in the Lepidoptera; it is confined primarily to Tineidae (fungus feeders), Elachistidae of the subfamily Depressariinae (fungus feeders), and primitive Noctuidae (dead leaf feeders). It also includes *Chytonix palliatricula* (Guenée), a noctuid species in the subfamily Hadeninae, which feeds on *Ustinaginales* (a smut) on *Aster* flowers (Rings et al. 1992). This is a most unusual food source for a noctuid species. The lichen and moss feeders are also a highly specialized group, restricted in this study to two stand generalist species of Arctiidae. The Salicaceae feeders are a large group represented by mature-stand and old-stand associates and stand generalists in a diverse array of higher taxonomic groups. This reflects the abundance of Salicaceae host plants (genera *Salix* and *Populus*) throughout the study area. Likewise, the small size and low abundance of the conifer feeding guild reflects the relative scarcity of *Picea* and other conifers in the study area. Only six species fell into the "unknown" feeding guild, which indicates that, for the most part, the common Lepidoptera species collected in this study are quite well known biologically.

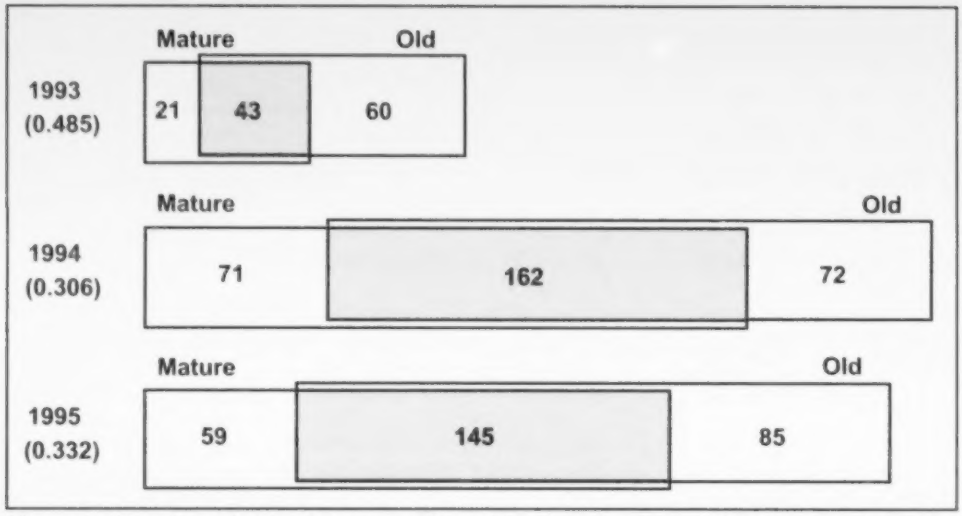

Figure 7. Number of shared (gray portion of bars) and unique (white portions) species collected in mature and old stands in 1993, 1994, and 1995 (bar lengths are proportional to the number of species). Numbers in parentheses for each year indicate beta diversity determined with Wilson and Shmida's (1984) calculations.

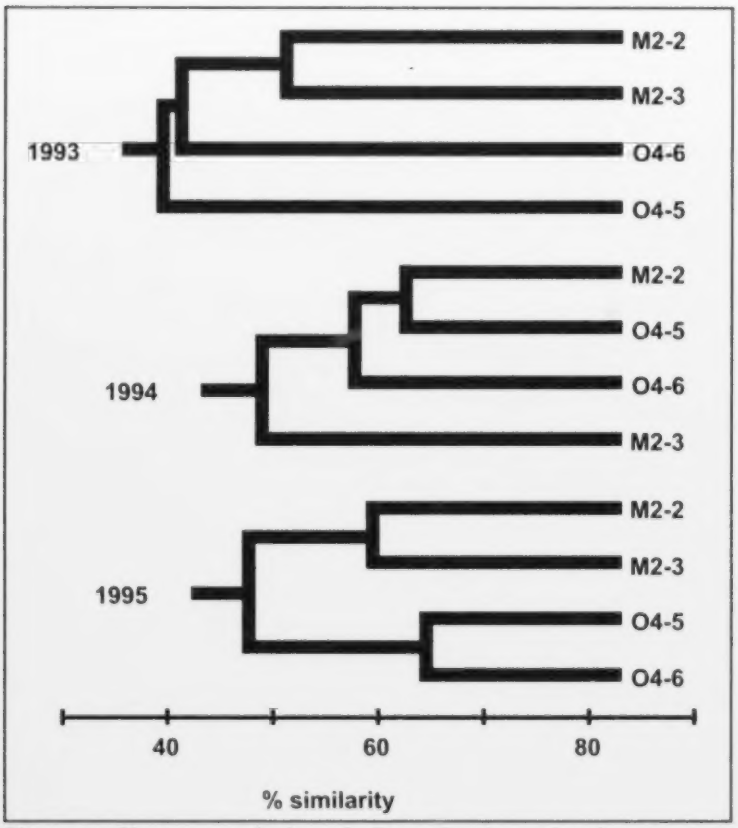

Figure 8. Cluster analysis of Bray–Curtis pair-wise percent similarities for Lepidoptera collected in 1993, 1994, and 1995. M2-2 and M2-3 designate sites in the mature stand; O4-5 and O4-6 designate sites in the old stand.

Table 5. Common species of Lepidoptera associated with aspen-dominated stands near Lac La Biche, Alberta

Family and species	*n*	IV or G	Host specificity	Feeding guild
Species associated with mature stands				
Gelechiidae				
Chionodes lugubrella (Fabricius)	28	75.0	Polyphagous	Generalist
Filatima abactella (Clarke)	12	91.7	Oligophagous	Salicaceae feeder
Tortricidae				
Apotomis removana (Kearfott)	19	94.7	Oligophagous	Salicaceae feeder
Geometridae				
Cabera variolaria Guenée	11	81.8	Oligophagous	Salicaceae feeder
Caripeta divisata Walker	13	84.6	Oligophagous	Conifer feeder
Xanthorhoe munitata (Hübner)	19	84.2	Polyphagous	Low and nonwoody plant feeder
Euphyia unangulata (Haworth)	15	93.3	Polyphagous	Low and nonwoody plant feeder
Noctuidae				
Zanclognatha lutalba (Smith)	11	100.0	Oligophagous	Fungus and dead leaf feeder
Catocala relicta Walker	52	90.4	Oligophagous	Salicaceae feeder
Nycteola frigidana (Walker)	10	80.0	Monophagous	Salicaceae feeder
Raphia frater Grote	249	96.0	Oligophagous	Salicaceae feeder
Parastichtis suspecta (Hübner)	21	76.2	Oligophagous	Salicaceae feeder
Chytonix palliatricula (Guenée)	24	91.7	Monophagous	Fungus and dead leaf feeder
Litholomia napaea (Morrison)	19	78.9	Monophagous	Salicaceae feeder
Brachylomia discinigra (Walker)	26	80.8	Oligophagous	Salicaceae feeder
Homohadena badistriga (Grote)	14	100.0	Monophagous	Woody plant feeder
Orthosia revicta (Morrison)	52	75.0	Oligophagous	General deciduous tree feeder
Egira dolosa (Grote)	39	89.7	Oligophagous	Salicaceae feeder
Cerastis salicarum (Walker)	17	82.4	Unknown	Unknown
Species associated with old stands				
Gracillariidae				
Caloptilia alnicorella (Chambers)	46	82.6	Monophagous	Salicaceae feeder
Caloptilia betulivora McDunnough	29	75.9	Monophagous	General deciduous tree feeder
Parornix conspicuella (Dietz)	60	88.3	Monophagous	Salicaceae feeder
Coleophoridae				
Coleophora pruniella Clemens	26	80.8	Monophagous	Woody plant feeder
Tortricidae				
Epinotia castaneana (Walsingham)	60	98.3	Monophagous	Woody plant feeder
Croesia albicomana (Clemens)	16	87.5	Monophagous	Woody plant feeder
Pandemis canadana Kearfott	66	75.8	Oligophagous	General deciduous tree feeder
Clepsis melaleucana (Walker)	68	83.8	Oligophagous	Low and nonwoody plant feeder
Drepanidae				
Drepana arcuata Walker	37	91.9	Oligophagous	Salicaceae feeder
Drepana bilineata (Packard)	29	86.2	Oligophagous	Salicaceae feeder
Oreta rosea (Walker)	13	84.6	Polyphagous	Generalist
Geometridae				
Protitame virginalis (Hulst)	12	75.0	Oligophagous	Salicaceae feeder
Macaria bitactata (Walker)	24	95.8	Polyphagous	Generalist
Iridopsis larvaria (Guenée)	32	75.0	Oligophagous	General deciduous tree feeder
Erannis tiliaria (Harris)	12	83.3	Oligophagous	Salicaceae feeder
Cabera erythemaria Guenée	108	76.9	Oligophagous	Salicaceae feeder
Besma quercivoraria (Guenée)	35	88.6	Oligophagous	Salicaceae feeder
Scopula frigidaria (Möschler)	13	76.9	Unknown	Unknown
Dysstroma hersiliata (Guenée)	142	83.8	Monophagous	Woody plant feeder
Xanthorhoe fossaria Taylor	20	75.0	Unknown	Unknown
Venusia cambrica Curtis	75	82.7	Oligophagous	Salicaceae feeder
Notodontidae				
Schizura leptinoides (Grote)	10	100.0	Monophagous	Salicaceae feeder
Noctuidae				
Acronicta innotata Guenée	15	86.7	Oligophagous	Salicaceae feeder
Acronicta fragilis (Guenée)	24	75.0	Monophagous	Salicaceae feeder
Phlogophora periculosa Guenée	29	82.8	Oligophagous	Conifer feeder

Table 5. Concluded

Family and species	*n*	IV or G	Host specificity	Feeding guild
Xylena curvimacula (Morrison)	10	80.0	Oligophagous	Salicaceae feeder
Anathix puta (Grote & Robinson)	29	75.9	Monophagous	Salicaceae feeder
Platypolia anceps (Stephens)	33	75.8	Monophagous	Low and nonwoody plant feeder
Generalists				
Tineidae				
Niditinea orleansella (Chambers)	14	0.91	Oligophagous	Fungus and dead leaf feeder
Gracillariidae				
Caloptilia stigmatella (Fabricius)	11	0.82	Monophagous	Salicaceae feeder
Gelechiidae				
Sinoe n. sp. 1	25	0.85	Unknown	Unknown
Chionodes occlusus (Braun)	40	0.77	Unknown	Unknown
Tortricidae				
Gypsonoma fasciolana (Clemens)	16	1.0	Oligophagous	Salicaceae feeder
Epinotia rectiplicana (Walsingham)	94	0.78	Oligophagous	Salicaceae feeder
Cydia populana (Busck)	31	0.84	Monophagous	Salicaceae feeder
Clepsis persicana (Fitch)	26	0.85	Polyphagous	Generalist
Ptycholoma virescana (Clemens)	173	0.84	Oligophagous	Woody plant feeder
Crambidae				
Eudonia albertalis (Dyar)	20	0.80	Unknown	Unknown
Synclita obliteralis (Walker)	52	0.77	Polyphagous	Low and nonwoody plant feeder
Phlyctaenia coronata (Hufn.)	30	0.78	Polyphagous	Woody plant feeder
Udea itysalis (Walker)	81	0.94	Monophagous	Low and nonwoody plant feeder
Geometridae				
Macaria loricaria (Eversmann)	93	0.75	Oligophagous	Salicaceae feeder
Ectropis crepuscularia (Denis & Schiffermüller)	35	0.79	Polyphagous	Generalist
Plagodis phlogosaria (Guenée)	14	0.81	Polyphagous	Generalist
Sicya macularia (Harris)	17	0.80	Polyphagous	Generalist
Cyclophora pendulinaria (Guenée)	74	0.93	Polyphagous	Generalist
Eulithis explanata (Walker)	41	0.79	Oligophagous	Conifer feeder
Hydriomena renunciata (Walker)	57	0.81	Oligophagous	General deciduous tree feeder
Spargania luctuata (Denis & Schiffermüller)	27	0.88	Monophagous	Low and nonwoody plant feeder
Anticlea vasiliata Guenée	66	0.92	Oligophagous	Woody plant feeder
Xanthorhoe abrasaria (Herrich-Schäffer)	17	0.94	Monophagous	Low and nonwoody plant feeder
Xanthorhoe ferrugata (Clerk)	18	0.78	Polyphagous	Low and nonwoody plant feeder
Sphingidae				
Smerinthus cerisyi Kirby	129	0.87	Oligophagous	Salicaceae feeder
Notodontidae				
Clostera albosigma Fitch	25	0.96	Oligophagous	Salicaceae feeder
Furcula scolopendrina (Boisduval)	44	0.85	Oligophagous	Salicaceae feeder
Arctiidae				
Eilema bicolor (Grote)	10	0.87	Oligophagous	Lichen and moss feeder
Clemensia albata Packard	40	0.83	Oligophagous	Lichen and moss feeder
Noctuidae				
Idia n. sp. nr. *aemula* Hübner	29	0.92	Oligophagous	Fungus and dead leaf feeder
Catocala unijuga Walker	52	0.77	Oligophagous	Salicaceae feeder
Lithacodia albidula (Guenée)	39	0.78	Oligophagous	Grass feeder
Enargia infumata (Grote)	117	0.86	Oligophagous	Salicaceae feeder
Polia nimbosa (Guenée)	48	0.83	Monophagous	Salicaceae feeder
Eurois occulta (Linnaeus)	57	0.85	Polyphagous	Woody plant feeder
Eurois astricta Morrison	115	0.84	Polyphagous	Woody plant feeder
Aplectoides condita (Guenée)	198	0.82	Oligophagous	Conifer feeder
Protolampra rufipectus (Morrison)	43	0.77	Polyphagous	Generalist

Note: IV = indicator value (species associated with mature or old stands) sensu Dufrêne and Legendre (1997), *G* = generalist value (generalist species) calculated as described in Materials and Methods.

Table 6. Numbers and percent of mature-stand and old-stand associates and of generalists, categorized by degree of host-plant specialization

Degree of host-plant specialization	No. (and percent) of species[a]		
	Mature-stand associates	Old-stand associates	Generalists
Monophagous	4 (21.1)	11 (39.3)	6 (15.8)
Oligophagous	11 (57.9)	13 (46.4)	18 (47.4)
Polyphagous	3 (15.8)	2 (7.1)	11 (28.9)
Unknown	1 (5.3)	2 (7.1)	3 (7.9)

[a]Percents are calculated on the basis of number of species in the particular category (mature-stand or old-stand associates, generalists).

Table 7. Numbers and percent of mature-stand and old-stand associates and of generalists, categorized by host-plant guild

Host-plant guild	No. (and percent) of species[a]		
	Mature-stand associates	Old-stand associates	Generalists
Grass feeders	0 (0.0)	0 (0.0)	1 (2.6)
Woody plant feeders	1 (5.3)	4 (14.3)	5 (13.2)
Low and nonwoody plant feeders	2 (10.5)	2 (7.1)	5 (13.2)
Fungus and dead leaf feeders	2 (10.5)	0 (0.0)	2 (5.3)
Salicaceae feeders	10 (52.6)	14 (50.0)	11 (28.9)
General deciduous tree feeders	1 (5.3)	3 (10.7)	1 (2.6)
Conifer feeders	1 (5.3)	1 (3.6)	2 (5.3)
Lichen and moss feeders	0 (0.0)	0 (0.0)	2 (5.3)
Generalists	1 (5.3)	2 (7.1)	6 (15.8)
Unknown	1 (5.3)	2 (7.1)	3 (7.9)

[a]Percents are calculated on the basis of number of species in the particular category (mature-stand or old-stand associates, generalists).

Comparison of Mature and Old Stands

Few clear differences in Lepidoptera communities were evident between the mature and old stands, because of high within-stand variation. The mature-stand community exhibited greater heterogeneity, but there were no clear differences in overall abundance or species richness. Because ecological pressures act on individual species, species-level distribution patterns in these stands were examined.

The old stand had a higher number and greater proportion of species unique to that stand, and a higher number of stand associates, than the mature stand. These differences suggest that old stands may have higher habitat diversity than mature stands. In fact, the findings of other studies that examined structural and other biodiversity components of these and other stands indicated that the old stands have larger (in terms of both diameter and height) and older trees, lower aspen density, higher birch and spruce density, more snags, a denser, more diverse tall understory layer, a higher proportion of fungi and moss cover, a higher overall diversity of low, mid, and upper strata plants, and a higher richness of nonvascular plants than mature stands (Stelfox 1995 and papers therein). These old stands are thus structurally and biologically more diverse than the mature stands. The higher plant diversity may explain why more old-stand associates than mature-stand associates were monophagous.

Many of the mature-stand and old-stand associates feed on aspen, which was abundant in both stands; this suggests that factors other than host-plant availability are at play. Chesterman and Stelfox (1995) found a slightly different temperature regime in mature and old stands because of differing light penetration. These temperature differences may affect Lepidoptera composition, either directly or indirectly through host-plant effects. This supposition is in keeping with the findings of Lepš et al. (1998), who noted that while some monophagous species were limited by food availability, the populations of oligophagous and polyphagous moths were limited by environmental factors other than food plant availability. Spruce bud moth (*Zeiraphera canadensis* Mutuura & Freeman) was not evaluated in the present study, because only one specimen was collected; however, Ostaff and Quiring (2000a, 2000b) found that populations of this species responded negatively to microclimatic conditions associated with crown closure as stands aged.

A number of species found to be associated with mature or old stands in the present study were found to be indicators of deciduous stands when compared to mixed and coniferous stands by Morneau (2002). These were the old-stand associates *Anathix puta* (Grote & Robinson), *Iridopsis larvaria* (Guenée), *Platypolia anceps* (Stephens), and *Protitame virginalis* (Hulst), and the mature-stand associates *Orthosia revicta* (Morrison) and *Brachylomia discinigra* (Walker). Although the Morneau (2002) study and the present study tested for specialization across different ecological variables, the results of both studies indicate that these species are not randomly distributed across the forest landscape.

Utility of Lepidoptera as an Indicator Group

Because so much of the biota of boreal forest ecosystems is made up of arthropods, which are poorly known, much biodiversity research for these ecosystems remains at the documentation stage. Lepidoptera constitute one of the groups that is well enough known to be adequately sampled and identified, but there is not enough information on their biology to know how they respond to environmental variables. Therefore, they cannot yet be used as environmental or ecological indicator species, at least according to the definitions of McGeoch (1998). Lepidoptera are also unproven as biodiversity indicators, because overall arthropod diversity cannot yet be measured well enough to test whether Lepidoptera diversity is an adequate surrogate. However, biodiversity information is urgently required for conservation decisions in the boreal forest (Simberloff 1999). Therefore, in this study Lepidoptera were used as biodiversity indicators sensu McGeoch (1998), without a strong empirical basis for their use, as advised by McGeoch (1998). It is the authors' hope that they are indicative of the diversity of other groups not yet considered. The working hypothesis is therefore that Lepidoptera diversity is correlated with overall species diversity.

Even though the utility of Lepidoptera as indicators remains largely untested, many species in the current study did indeed show an affinity for either the mature stand or the old stand, whereas other species appeared to be habitat generalists. Although these results do not allow patterns to be linked unequivocally to the underlying environmental parameters, further examination of Lepidoptera for use as an indicator group would be worthwhile. They appear to show habitat preferences that, given enough background ecological information, might allow accurate predictions about their response to environmental disturbance. However untested they may be, they provide one of the few tools now available to predict the effects of habitat changes.

The distribution of mature-stand and old-stand associates and stand generalists among taxonomic subgroups within the Lepidoptera can also be examined. The Geometroidea and Drepanoidea (Table 8) showed particular promise for use as indicators. Many species of these superfamilies had a particular affinity for old stands; 46% of the old-stand associates were members of these taxa. These superfamilies were relatively common in this study, accounting for 25.5% of all specimens collected. Of the 79 species collected, only 6 were represented by singletons and 5 by doubletons; 40 were common enough to assess habitat affinities. The Chao-1 estimate of total richness for this group was 82.6 ± 3.2 species, indicating that almost all of the UV-attracted species present in the study area were indeed collected. These moths are well known taxonomically and biologically (McGuffin 1967, 1972, 1977, 1981, 1987, 1988; Bolte 1990), are relatively common, are easily sampled, are not generally long-distance dispersers, and appear to be responsive enough to environmental variables that the group would be an excellent candidate as an environmental or ecological indicator group (Scoble 1992; Thomas 2001, 2002; Morneau 2002). Of particular interest is the subfamily Drepaninae: of the four species known to occur in Alberta, three were collected in this study, all of which were deemed old-stand associates.

Of the 102 noctuid moth species collected, 40 were common enough for habitat affinities to be assessed. Twelve of these were deemed to be mature-stand associates (Table 8). Although many species were represented by singletons and doubletons (16 and 14, respectively), the total community was reasonably well sampled (Chao-1 estimate of total richness = 111.1 ± 5.1). Noctuids tend to be strong, large-bodied fliers (Scoble 1992). Therefore, many UV-collected specimens may be strays or transients, adding variance to the data. This factor, coupled with incomplete knowledge of their taxonomy and biology, make them less promising than the Geometroidea and Drepanoidea as an indicator group. Nevertheless, they provide some evidence of habitat specialization.

Macrolepidoptera other than the Geometroidea, Drepanoidea, and Noctuidae included several rare species and thus were incompletely sampled (Chao-1 = 37.5 ± 11.6). Among the species common enough to allow analysis of habitat preferences, a high proportion were generalists (Table 8), and only one species showed any stand association. This group as a whole does not appear to be as useful as the Geometroidea and Drepanoidea or the Noctuidae as indicators.

Many of the microlepidoptera (primitive moths, monotrysian groups, and the lower ditrysian superfamilies sensu Kristensen [1999]) are highly host-specific and are generally not strong fliers (Scoble 1992). These traits appear to make them good candidates as an indicator group. They made up a higher proportion of the catch in the more complex old stand (38.2%) than in the mature stand (28.2%). However, despite accounting for almost half of the overall richness (47.6%), many were rare species, including 63 singletons and 26 doubletons. The total richness of this group has been far from thoroughly sampled (Chao-1 = 263.3 ± 20.3). The relative rarity of many species renders them difficult to collect in adequate numbers to permit statistical analyses of relative abundances. Only 38 species were common enough that they could be assessed for habitat specialization. Eleven species were deemed to have habitat affinities, 3 to the mature stand and 8 to the old stand (Table 8). Despite some of the species in this group showing stand associations, most were relatively rare, and many are poorly known taxonomically and difficult to identify. These factors render them not very promising for use as an indicator group. Therefore, it is recommended that the macrolepidoptera be explored and tested further for their indicator value and that particular attention be paid to the Geometroidea and Drepanoidea.

Table 8. Average indicator value[a] and generalist value, and number and percent of species designated as mature-stand and old-stand associates and as generalists, for taxonomic subgroups of Lepidoptera

Taxonomic subgroup	No. of species	Average indicator value	No. (and percent)[b] Mature-stand associates	Old-stand associates	Average generalist value	No. (and percent) of generalists
Microlepidoptera						
Tortricidae	17	71.6	1 (5.9)	4 (23.5)	0.677	5 (29.4)
Pyraloidea	7	60.8	0 (0.0)	0 (0.0)	0.780	4 (57.1)
Other microlepidoptera	14	69.4	2 (14.3)	4 (28.6)	0.634	4 (28.6)
Total	38	68.8	3 (7.9)	8 (21.1)	0.680	13 (34.2)
Macrolepidoptera						
Geometroidea and Drepanoidea	40	69.1	4 (10.0)	13 (32.5)	0.640	11 (27.5)
Noctuidae	40	72.3	12 (30.0)	6 (15.0)	0.621	9 (22.5)
Other macrolepidoptera	12	65.0	0 (0.0)	1 (8.3)	0.733	5 (41.7)
Total	92	70.0	16 (17.4)	20 (21.7)	0.644	25 (27.2)

[a]Sensu Dufrêne and Legendre (1997).
[b]Percents are calculated with respect to number of species in the particular taxonomic subgroup.

Summerville et al. (2003) examined the utility of several moth families and subfamilies as indicators of overall Lepidoptera diversity in eastern deciduous forests. Their results were significantly different from those of the present study. They found that the Arctiidae constituted the best indicator of overall moth species richness and that the Notodontidae represented the best indicator of coarse-scale disturbance. The eastern deciduous forest of their study exhibited much higher diversity of Arctiidae and Notodontidae, and lower diversity and ecological fidelity of Geometridae, than the boreal mixedwood forest of the present study. Applying their criteria to the moth fauna of the boreal mixedwood, Geometridae would be ranked as having the best indicator value. This comparison illustrates the fact that indicator groups suitable for one type of forest are not necessarily appropriate for other forest types.

Implications for Forest Harvesting

If old forest stands become a lesser component of the managed forest landscape, many of the Lepidoptera species associated with old stands may be adversely affected. To conserve the full complement of Lepidoptera diversity, harvesting and management practices should be designed to retain a mix of stand ages, including older, postrotational stands, on the landscape. To measure the effects of these practices on the forest landscape, macrolepidoptera show promise as ecological and biodiversity indicators.

ACKNOWLEDGMENTS

Héctor Cárcamo, Tom Clark, James Hammond, Rob Lucas, Phillippa Rodriguez, Peter Shipley, the late Tim Spanton, Kevin Sytsma, and Daryl Williams assisted with field collecting. The Alberta Land and Forest Service (Lac La Biche Region) provided field accommodation, and the Alberta Research Council provided maps and assisted with site selection. Gary Anweiler, Klaus Bolte, Peter Dang, Ron Hodges, Don Lafontaine, and A. Doug Macaulay assisted with identification of collected specimens. Lakeland Provincial Park and Alberta-Pacific Forest Industries Inc. cooperated and permitted access for collecting. This manuscript benefited from comments by Jan Volney and James Hammond of the Canadian Forest Service in Edmonton and Peter Mason of Agriculture and Agri-Food Canada in Ottawa. Funding was supplied by the Canada–Alberta Partnership Agreement in Forestry, the Canadian Forest Service, and a Natural Sciences and Engineering Research Council operating grant (to John Spence).

LITERATURE CITED

Adamski, D.; Peters, T.M. 1986. Review of nearctic *Apotomis* Hübner (Lepidoptera: Tortricidae: Olethreutini). Can. Entomol. 118:649–689.

Beaudry, S.; Duchesne, L.C.; Cote, B. 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. Can. J. For. Res. 27:2065–2071.

Beckingham, J.D.; Archibald, J.H. 1996. Field guide to ecosites of northern Alberta. Nat. Resour. Can., Can. For. Serv., Northwest Reg., North. For. Cent., Edmonton, AB. Spec. Rep. 5.

Bolte, K.B. 1990. Guide to the Geometridae of Canada (Lepidoptera) VI. Subfamily Larentiinae I. Revision of the genus *Eupethecia*. Mem. Entomol. Soc. Can. 151.

Bonan, G.B.; Shugart, H.H. Jr. 1989. Environmental factors and ecological processes in boreal forests. Annu. Rev. Ecol. Syst. 20:1–28.

Bray, J.R.; Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.

Brown, R.L. 1980. A revision of the genus *Epinotia* (Hübner) (Tortricidae: Eucosmini), Part 1: The North American species of the *stroemiana* lineage. PhD thesis, Cornell Univ., Ithaca, NY.

Brzustowski, J. 1999. [Statistics programs by John Brzustowski] [on-line]. <http://www.biology.ualberta.ca/jbrzusto/index.html>. Accessed 16 Dec. 2002.

Chao, A.; Lee, S.M. 1992. Estimating the number of classes via sample coverage. J. Am. Stat. Assoc. 87:210–217.

Chesterman, D.; Stelfox, J.B. 1995. Relationships between microclimate and stand age and structure in aspen mixedwood forests in Alberta. Pages 13–27 *in* J.B. Stelfox, ed. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alta. Environ. Cent., Vegreville, AB (AECV95-R1); Can. For. Serv., Northwest Reg., Edmonton, AB (Project 0001A).

Colwell, R.K.; Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans. Ser. B 345:101–118.

Danks, H.V. 1979. Summary of the diversity of Canadian terrestrial arthropods. Pages 240–244 *in* H.V. Danks, ed. Canada and its insect fauna. Mem. Entomol. Soc. Can. 108.

Danks, H.V.; Foottit, R.G. 1989. Insects of the boreal zone of Canada. Can. Entomol. 121:625–690.

Dufrêne, M.; Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345–366.

Forbes, W.T.M. 1923. The Lepidoptera of New York and neighboring states. Part I. Primitive forms, microlepidoptera, pyraloids, bombyces. Cornell Univ. Agric. Exp. Stn. Mem. 68:1–729.

Forbes, W.T.M. 1948. The Lepidoptera of New York and neighboring states. Part II. Geometridae, Sphingidae, Notodontidae, Lymantriidae. Cornell Univ. Agric. Exp. Stn. Mem. 274:1–263.

Freeman, T.N. 1958. The Archipinae of North America (Lepidoptera: Tortricidae). Mem. Entomol. Soc. Can. 7.

Hammond, H.E.J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. Can. Entomol. 129:1009–1033.

Hammond, H.E.J.; Langor, D.W.; Spence, J.R. 2002. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Can. J. For. Res. 31:1175–1183.

Handfield, L. 1999. Le guide des papillons du Québec (version scientifique). Vol. 1. Broquet, Boucherville, QC.

Hodges, R.W. 1999. Gelechioidea: Gelechiidae (part): Gelechiinae (part — *Chionodes*). Fascicle 7.6 *in* R.B. Dominick, D.C. Ferguson, J.G. Franclemont, R.W. Hodges, and E.G. Munroe, eds. The moths of America north of Mexico. Wedge Entomological Research Foundation, Washington, DC.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology (Wash. DC.) 52: 577–586.

Jones, J.R.J.L. 1951. An annotated checklist of the macrolepidoptera of British Columbia. Entomol. Soc. B.C. Occas. Pap. 1.

Krebs, C.J. 1989. Ecological methodology. Harper Collins Publishers, New York, NY.

Kristensen, N.P., ed. 1999. Lepidoptera, moths and butterflies. Vol. 1. Evolution, systematics, and biogeography. Handbook of zoology. Vol. 4 (Arthropoda: Insecta), part 35. Walter de Gruyter, Berlin, Germany.

Lafontaine, J.D. 1998. Noctuoidea: Noctuidae (part): Noctuinae: Noctuini. Fascicle 27.3 *in* R.B. Dominick, D.C. Ferguson, J.G. Franclemont, R.W. Hodges, and E.G. Munroe, eds. The moths of America north of Mexico. Wedge Entomological Research Foundation, Washington, DC.

Lafontaine, J.D.; Wood, D.W. 1997. Butterflies and moths (Lepidoptera) of the Yukon. Pages 723–785 *in* H.V. Danks and J.A. Downes, eds. Insects of the Yukon. Biol. Sur. Can. (Terrestrial Arthropods), Ottawa, ON.

Lawton, J.H.; Bignell, D.E.; Bolton, B.; Bloemers, G.F.; Eggleton, P.; Hammond, P.M.; Hodda, M.; Holt, R.D.; Larsen, T.B.; Maudsley, N.A.; Stork, N.E.; Srivastava, D.S.; Watte, A.D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forests. Nature (Lond.) 391:72–76.

Leps, J.; Spitzer, K.; Jaroš, J. 1998. Food plants, species composition and variability of the moth community in undisturbed forest. Oikos 81:538–548.

Magurran, A.E. 1985. The diversity of macrolepidoptera in two contracting woodland habitats at Banagher, Northern Ireland. Proc. R. Ir. Acad. Sect. B Biol. Geol. Chem. Sci. 85:121–132.

Maser, C. 1994. Sustainable forestry: philosophy, science and economics. St. Lucie Pr., Delray Beach, FL.

McDunnough, J.H. 1946. Gracillariid studies (Gracillariidae, Lepidoptera). Can. Entomol. 78:91–95.

McGeoch, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. Biol. Rev. (Camb.) 73:181–201.

McGuffin, W.C. 1967. Guide to the Geometridae of Canada (Lepidoptera) I. Subfamily Sterrhinae. Mem. Entomol. Soc. Can. 50.

McGuffin, W.C. 1972. Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. 1. Mem. Entomol. Soc. Can. 86.

McGuffin, W.C. 1977. Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. 2. Mem. Entomol. Soc. Can. 101.

McGuffin, W.C. 1981. Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. 3. Mem. Entomol. Soc. Can. 117.

McGuffin, W.C. 1987. Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. 4. Mem. Entomol. Soc. Can. 138.

McGuffin, W.C. 1988. Guide to the Geometridae of Canada (Lepidoptera) III, IV and V. Subfamilies Archiearinae, Oenochrominae, and Geometrinae. Mem. Entomol. Soc. Can. 145.

Miller, W.E. 1987. Guide to the olethreutine moths of midland North America (Tortricidae). US Dep. Agric., For. Serv., North Cent. For. Exp. Stn., St. Paul, MN. Agric. Handb. 660.

Morneau, L. 2002. Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta. M.Sc. thesis, Univ. Alberta, Edmonton, AB.

Morris, R.F. 1980. Butterflies and moths of Newfoundland and Labrador. Agric. Can. Res. Branch, Res. Stn., St. John's, NF. Publ. 1691.

Munroe, E. 1976. Pyraloidea: Pyralidae (Part) Fascicle 13.2A *in* R.B. Dominick, D.C. Ferguson, J.G. Franclemont, R.W. Hodges, and E.G. Munroe, eds. The moths of America north of Mexico. Wedge Entomological Research Foundation, Washington, DC.

Niemelä, J.; Langor, D.W.; Spence, J.R. 1993a. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conserv. Biol. 7:521–560.

Niemelä, J.; Spence, J.R.; Langor, D.W.; Haila, Y.; Tukia, H. 1993b. Logging and boreal ground-beetle assemblages on two continents: implications for

conservation. Pages 29–50 *in* K.J. Gaston, T.R. New, and M.J. Samways, eds. Perspectives on insect conservation. Intercept, Andover, UK.

Ostaff, D.P.; Quiring, D.T. 2000a. Population trends of a specialist herbivore, the spruce bud moth, in young white spruce stands. Can. Entomol. 132:825–842.

Ostaff, D.P.; Quiring, D.T. 2000b. Role of the host plant in the decline of populations of a specialist herbivore, the spruce bud moth. J. Anim. Ecol. 69:262–273.

Peterson, E.B.; Peterson, N.M. 1992. Ecology, management and use of aspen and balsam poplar in the prairie provinces, Canada. For. Can., Northwest Reg., North. For. Cent., Edmonton, AB. Spec. Rep. 1.

Pielou, E.C. 1969. An introduction to mathematical ecology. Wiley Interscience Publ., New York, NY.

Pielou, E.C. 1977. Mathematical ecology. Wiley Interscience Publ., New York, NY.

Pohl, G.R.; Landry, J.-F.; Langor, D.W.; Spence, J.R. n.d. Moths and butterflies (Lepidoptera) of the boreal mixedwood forest near Lac La Biche, Alberta, including new provincial records. Can. Field-Nat. Forthcoming.

Pratt, L.; Urquhart, I. 1994. The last great forest. Newest Pr., Edmonton, AB.

Prentice, R.M. 1962. Forest Lepidoptera of Canada reported by the Forest Insect Survey. Vol. 2: Nycteolidae, Notodontidae, Noctuidae, Liparidae. Can. Dep. For., For. Entomol. Pathol. Branch, Ottawa, ON. Bull. 128.

Prentice, R.M. 1963. Forest Lepidoptera of Canada reported by the Forest Insect Survey. Vol. 3: Lasiocampidae, Drepanidae, Thyatiridae, Geometridae. Can. Dep. For., For. Entomol. Pathol. Branch, Ottawa, ON. Publ. 1013.

Prentice, R.M. 1965. Forest Lepidoptera of Canada reported by the Forest Insect Survey. Vol. 4: Microlepidoptera. Can. Dep. For., Ottawa, ON. Publ. 1142.

Razowski, J. 1966. World fauna of the Tortricini (Lepidoptera: Tortricidae). Panstwow Wydawnictwo Naukowe, Krakow, Poland.

Rings, R.W.; Metzler, E.H.; Arnold, F.J.; Harris, D.H. 1992. Owlet moths of Ohio — order Lepidoptera — family Noctuidae. Ohio Biol. Surv. Bull. 9:1–219.

Rockburne, E.W.; Lafontaine, J.D. 1976. The cutworm moths of Ontario and Quebec. Can. Dep. Agric., Ottawa, ON. Publ. 1593.

Sanders, H.L. 1968. Marine benthic diversity: a comparative study. Am. Nat. 102:243–282.

Sargent, T.D. 1976. Legion of night — the underwing moths. Univ. Massachusetts Pr., Amherst, MA.

Scoble, M.J. 1992. The Lepidoptera. Form, function and diversity. Oxford University Pr., Oxford, UK.

Simberloff, D. 1989. The role of science in the preservation of forest biodiversity. For. Ecol. Manage. 115:101–111.

Spence, J.R.; Langor, D.W.; Hammond, H.E.J.; Pohl, G.R. 1997. Beetle abundance and diversity in a boreal mixedwood forest. Pages 287–301 *in* A.D. Watt, N.E. Stork, and M.D. Hunter, eds. Forests and insects. Chapman and Hall, London, UK.

Spence, J.R.; Langor, D.W.; Niemelä, J.; Cárcamo, H.; Currie, C.R. 1996. Northern forestry and carabids: the case for concern about old-growth species. Ann. Zool. Fenn. 33:173–184.

Stelfox, J.B., ed. 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alta. Environ. Cent., Vegreville, AB (AECV95-R1); Can. For. Serv., Northwest Reg., Edmonton, AB (Project 0001A).

Summerville, K.S.; Ritter, L.M.; Crist, T.O. 2003. Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. Biol. Conserv. 116:9–18.

Thomas, A.W. 2001. Moth diversity in a northeastern, North American, red spruce forest. I. Baseline study. Nat. Resour. Can., Can. For. Serv., Atlantic For. Cent., Fredericton, NB. Inf. Rep. M-X-210E. 42 pp.

Thomas, A.W. 2002. Moth diversity in a northeastern, North American, red spruce forest. II. The effect of silvicultural practices on geometrid diversity (Lepidoptera: Geometridae). Nat. Resour. Can., Can. For. Serv., Atlantic For. Cent., Fredericton, NB. Inf. Rep. M-X-213E. 25 pp.

Wilson, M.V.; Shmida, A. 1984. Measuring beta diversity with presence–absence data. J. Ecol. 72:1055–1064.

Wolda, H. 1981. Similarity indices, sample size and diversity. Oecologia (Berl.) 50:296–302.

Young, M. 1997. The natural history of moths. T. and A.D. Poyser, London, UK.